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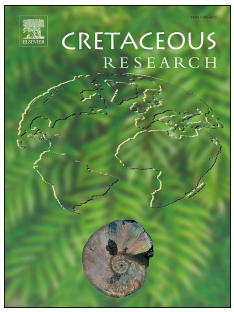

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Garrouste wrote the paper

Pouillon wrote the paper and prepared the specimen

Nel wrote the paper, searched the references, and made the analyses

The first predatory dance fly of the subfamily Ocydromiinae with specialized, raptorial legs in mid–Cretaceous amber from Myanmar (Diptera: Hybotidae)

Running head

mid–Cretaceous hunter dance fly

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ABSTRACT

The first ocydromiine hybotid fly is described and illustrated from a remarkable male preserved in mid-Cretaceous amber from northern Myanmar. *Pouillonhybos venator*, gen. et

sp. nov., is distinguished from other members of the subfamily Ocydromiinae as well as other lineages of living and fossil Hybotidae. The holotype of *P. venator* exhibits spectacular specializations of the mid and hind legs, modifications likely linked to the grasping of prey either during capture and/or while feeding. The species reported here is the earliest evidence of significant leg modifications in Hybotidae indicating an early appearance of such specializations in the family's history.

Keywords: Brachycera; Cenomanian; Empidoidea; predatory dance flies; taxonomy

1. Introduction

The family Hybotidae largely includes predaceous flies that typically frequent on fallen logs or semi-aquatic vegetation in forested environments. Although generally predators, a few are known to feed on pollen. Where known for the predatory taxa, many species capture preys while in flight although tachydromiines more readily subdue their prey on plant surfaces (Chvála, 1983). During feeding, hybotids grasp the prey item with their hind legs while manipulating their food and stabilizing themselves with their fore and midlegs (Wilder, 1974). Accordingly, various modifications of the hind legs have arisen among Hybotidae which appear to be associated with capturing and holding their prey, the most elaborate of which belong to groups believed to take their victims while in flight. The fossil record of the family is scanty, with comparatively few records (Evenhuis, 1994). . Hybotid flies are quite rare in the Mesozoic, with only the Early Cretaceous genus *Pseudoacarterus* Waters, 1989, the mid–Cretaceous *Electrocyrtoma* Cockerell, 1917, and the Late Cretaceous *Archiplatypus* Kovalev, 1974. Herein we report from the mid–Cretaceous Burmese amber a remarkable new hybotid fly of the subfamily Ocydromiinae with highly specialized male hind legs, implying that the

evolution of such features appeared early in the family's history. We provide a description of this new taxon and comparisons with the diversity of modern and other extinct genera.

2. Material and methods

The specimen comes from the earliest Cenomanian amber (98.79 ± 0.62 Ma, based on U-Pb zircon dating of the volcanoclastic matrix; Shi et al., 2012); location map of amber-bearing locality in Yin et al. (2018: fig. 1A). It is preserved in a piece of clear, yellow amber. The amber piece was cut, shaped, and polished using a diamond disk under water and diatomite, and was then mounted between two coverslips with sugar medium dissolved at saturation in water, before being examined and photographed. The inclusion was examined and measured under incident light with an Olympus SZX9 and Leitz Wetzlar binocular microscopes. The holotype is deposited in the amber collection of the Musée d'Histoire Naturelle et d'Ethnographie de Colmar (MHNEC), France under collection number MHNE.2020.7.1. We follow the terminology of Cumming & Wood (2009) and the empidoid classification of Sinclair & Cumming (2006).

3. Systematic palaeontology

Order Diptera Linnaeus, 1758

Superfamily Empidoidea Latreille, 1809

Family Hybotidae Meigen, 1820

Subfamily Ocydromiinae Schiner, 1862

Genus ***Pouillonhybos*** Ngô-Muller, Engel & Nel, gen. nov.

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Type species: *Pouillonhybos venator* Ngô-Muller, Engel & Nel, sp. nov.

Diagnosis. Proboscis short, oriented ventrally. Antenna with stylus elongate, arista-like, longer than postpedicel. Protibial gland present. Mesofemur crassate, with four stout, elongate, ventral setae; mesotibia elongate, basally slightly geniculate, with two outer rows of short, oblique setae and a single, elongate, apical spur. Hind legs greatly modified; metacoxa with one elongate seta; metafemur with pronounced inner curvature, with two stout, thickened, elongate subapical spines and a series of stout, elongate setae ventrally as well as a row of shorter, curved prolateral (ectal) setae; metatibia strongly arched with a prominent, thick, subapical, hook-like lobe, and a row of long inner setae, and an apical spur; metabasitarsus broadened, with an ectal row of curved setae and an ental row of long, rather straight setae. Wings well developed, much longer than abdomen; pterostigma lacking; C terminating at wing apex, on M_1; stem of Rs short; R_{2+3} comparatively straight; R_{4+5} and M_1 roughly parallel; *dm* present, elongate; m-m arched, with faint nebulous trace of M_2, trace disappearing after length about 0.5× m-m length; two veins emitted from *dm* reaching wing margin (M_1 and M_4); *cua* present, elongate, about as long as *bm*, with apex oblique, with outer angle obtuse, without spur vein; vein dm-m strongly oblique; CuA not broadly arching apically to CuA+CuP; CuP and CuA+CuP faint, not reaching wing margin; anal lobe narrow; alula absent. Epandrium with pair of articulated surstyli apically.

Etymology. The new generic name is a combination of the surname Pouillon, honoring Jean-Marc Pouillon, who donated the type specimen, and *Hybos* Meigen, the type genus of the family. The gender of the name is masculine.

Pouillonhybos venator Ngô-Muller, Engel & Nel, sp. nov.

Figs 1–3

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Etymology. The specific epithet is taken from the Latin word '***venator***', meaning, 'hunter', referring to the specialized metatibiae of this species.

Material. Holotype MHNE.2020.7.1 (a complete specimen in amber, coll. Jean-Marc Pouillon); Musée d'Histoire Naturelle et d'Ethnographie de Colmar, France.

Horizon and locality. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; lower Cenomanian, mid-Cretaceous.

Diagnosis. As for genus; only one included species.

Description. Male, body 2.03 mm long (Fig. 1); head 0.22 mm long, 0.30 mm wide; compound eyes apparently setose, with few visible very short setae, large, meeting at one point above (a gas bubble occludes views of the upper part of the head); ptilinal fissure absent; occiput and frons bare; apex of antenna with lengthened, arista-like stylus (Fig. 3A), possibly dimerous as a very short structure is present between it and postpedicel, apical on postpedicel; postpedicel pear-shaped, 0.06 mm long, quite shorter than stylus (0.66 mm long) and shorter than pedicel; pedicel with an apical crown of strong setae, longer than scape; proboscis short, oriented ventrad.

Thorax 0.64 mm long, 0.45 mm wide, with bare laterotergite; two elongate setae on scutellum and three near base of wing.

Wing hyaline (Fig. 1B), longer than abdomen, apex rounded, 2.22 mm long, 0.45 mm wide, covered with microtrichia, without darkened pterostigma; Sc ending on C, 1.08 mm from wing base; C extending to wing apex, terminating at apex of M1; Rs originating well distad level of humeral vein (h), 0.39 mm from it; branches of Rs not strongly thickened and crowded anterobasally; R2+3 elongate and straight, 0.08 mm long; R4+5 unbranched, 1.29 mm long, nearly straight and parallel to M1; cell *dm* present, 0.69 mm long, 0.13 mm wide, with three veins distally emerging from it: M1 (0.6 mm long), M2 (present as an exceedingly faint nebulous vein disappearing well before wing margin, distinctly shorter than m-m

crossvein), and M4 (0.19 mm long); CuA forming a distinct angle with basal part of CuP; cell *cua* scarcely shorter than cell *bm* (bm-cm and CuA nearly confluent), with outer angle obtuse; CuA+CuP vein not reaching wing margin; narrow anal lobe, 0.13 mm wide; lunule absent; a series of long setae on anal margin; haltere elongate, 0.41 mm long, 0.08 mm wide.

Legs (Figs 2, 3A). Pretarsal claws simple, empodia setiform; protibial gland present; profemur 0.29 mm long, 0.06 mm wide, curved, with a series of at least five long setae along inner surface; protibia 0.29 mm long, 0.04 mm wide, with three rows of stout setae, one apical spur; probasitarsus elongate, 0.18 mm long, with two series of long setae; protarsomere II 0.11 mm long; protarsomere III 0.08 mm long; protarsomere IV 0.04 mm long; protarsomere V 0.06 mm long; mesofemur crassate, approximately 0.42 mm long, 0.06 mm wide, with four stout, thickened, erect, spine-like setae on ventral surface; mesotibia 0.53 mm long, 0.04 mm wide, basally geniculate, with two series of rather short, oblique setae, a single elongate apical spur; mesotarsus ca. 0.53 mm long; metacoxa with a single, elongate, posteroventral seta, 0.29 mm long; metafemur 0.76 mm long, 0.09 mm wide, with a pronounced inner curvature and two stout, thickened, enlarged, subapical spurs (0.16 mm long) and a series of long, stout, erect, spine-like setae along ventral surface, a series of shorter, finer, curved, oblique setae along dorsal surface (Fig. 2); metatibia basally geniculate, strongly curved, with a subapical hook-like lobe (0.1 mm long), apex of lobe narrowly rounded, a row of long, oblique setae on inner surface, a single, short, basally thickened apical spur, outer surface with a row of erect to semierect, short, fine setae; metabasitarsus greatly broadened and somewhat trapezoidal as lateral margins slightly converge apically, 0.09 mm long, 0.04 mm wide, outer edge with a row of short, strongly curved setae, inner edge with a row of longer, obliquely erect, largely straight setae; metarsomere II elongate, 0.16 mm long, 0.01 mm wide, with two rows of fine, long setae; metataresomere III 0.09 mm long, 0.01 mm wide, metatarsomere IV 0.08 mm long, 0.008 mm wide, metatarsomere V 0.08 mm long, 0.008 mm wide.

Abdomen elongate (Fig. 2), rather narrow, 1.0 mm long, 0.24 mm wide, with a single, elongate spine-like seta laterally on segments II–V; male terminalia asymmetrical and rotated 90° (Fig. 3B); cercus thin with a small inner extension; hypoproct small near cercal base; phallus large, as long as and broader than cerci; epandrium greatly enlarged, spoon-shaped, apparently with an apical pair of articulated surstyli.

Female unknown.

4. Discussion

Pouillonhybos gen. nov. can be placed within the Empidoidea owing to the following characters: ptilinal fissure and lunule absent; empodia setiform; pedicel shorter than flagellum; flagellum with three flagellomeres; cell *cua* small; stylus elongate and thin; wing apex rounded; branches of R not strongly thickened and crowded anterobasally; C extending to wing apex; CuA+CuP not reaching wing margin. Using those traits outlined by recent authors (*e.g.*, Steyskal & Knutson, 1981; Sinclair & Cumming, 2006, 2017), the new fossil genus falls among the Hybotidae based on the following characters: apex of antenna with lengthened, bristle-like stylus (stylus also not setulose); thorax with bare laterotergite; protibial gland present; C ending at wing apex, instead of circumambient (but some empidids also have a costa terminating at the wing apex); Rs originating well distal to level of humeral vein (h); R4+5 unbranched; CuA forming a distinct angle with basal part of CuP. It should be noted that some Empididae have a wing venation quite similar to that of *Pouillonhybos* (viz. *Macrostomus* Wiedemann, 1817), especially in the narrow anal lobe and shape of cell *cua*, and even in the C terminating on M1. Such empidids, however, differ from *Pouillonhybos* in the setulose scape (not so in the fossil), shape of the more elongate flagellum, and, in the case of *Macrostomus*, lacking a defined stylus (Smith, 1961: fig. 3; Rafael & Cumming, 2004: figs 1, 3).

Wahlberg & Johanson (2018) presented a molecular phylogenetic analysis of the Empidoidea, in which Hybotidae are subdivided into six subfamilies: Bicellariinae Sinclair & Cumming, 2006; Ocydromiinae Schiner, 1862; Oedaleinae Chvála, 1983; Hybotinae Meigen, 1820; Tachydromiinae Meigen, 1822; and Trichininae Chvála, 1983. Most recently, Sinclair (2019) added the subfamily Stuckenbergomyiinae Sinclair, 2019. Affinities between the new fossil and Trichininae (*Trichinomyia* Tuomikoski, 1959 and *Trichina* Meigen, 1830) are excluded because of the absence of an alula, the narrow anal lobe, the absence of a pterostigma, and the elongate stylus (Tuomikoski, 1959). The Tachydromiinae are excluded because M_2 is present, albeit only as a short, faintly nebulous vein, cell *dm* present, and cell *cua* elongate (Sinclair & Cumming, 2006, 2017). Similarly, the subfamily Bicellariinae (*Bicellaria* Macquart, 1823) can be discounted owing to the narrow anal area and presence of cell *dm* (Kato, 1971). The Oedaleinae have a branched M_{1+2} and an anterad projecting proboscis, quite unlike *Pouillonhybos*, and the Stuckenbergomyiinae differ from the new fossil genus in the truncate cell *cua*, shortened stylus, and three veins emitted from cell *dm*.

Affinities with the Hybotinae would also be excluded because of the presence of M_2 in *Pouillonhybos*, but as it is rudimentary in the present fossil we prefer to compare the new genus to extant and fossil hybotine genera. The short proboscis of *Pouillonhybos* excludes affinities with *Syneches* Walker, 1852 (incl. *Parahybos* Kertész, 1899, *Harpamerus* Bigot, 1859, and *Epiceia* Walker, 1860), *Hybos* Meigen, 1803, *Smithybos* Ale-Rocha, 2000, *Syndyas* Loew, 1857, and *Lactistomyia* Melander, 1902. In the genera *Afrohybos* Smith, 1967, *Cerathybos* Bezzi, 1909, *Euhybus* Coquillett, 1895, and *Neohybos* Ale-Rocha & Carvalho, 2003 cell *cua* extends far distal to cell *bm* (Melander, 1902; Smith, 1967; Ale-Rocha, 2000, 2002, 2008; Ale-Rocha & Carvalho, 2003; Grootaert & Yang, 2009; Sinclair, 1996, 2011; Liu et al., 2012, 2014), quite unlike *Pouillonhybos* in which these cells are about subequal in length, with *cua* only scarcely shorter than *bm*. *Acarterus* Loew, 1858, *Lamachella* Melander,

1928, and the Cretaceous genus *Pseudoacarterus* Waters, 1989 have cell *cua* apically convex (*i.e.*, CuA is convexly arched), while in the new genus CuA is straight and oblique (Waters, 1989; Sinclair, 1996). Additionally, in *Lamachella* *cua* is distinctly shorter than *bm*, a pterostigma is usually present, m-cu is more elongate and not in near alignment with CuA, and R_{2+3} is sinuate, unlike *Pouillonhybos* (Smith, 1969: figs 137-138; Sinclair & Cumming, 2017). *Chillcottomyia* Saigusa, 1986, *Stenoproctus* Loew, 1858, and the Miocene genus *Syneproctus* Solórzano-Kraemer et al., 2020 have cell *cua* quite shorter than *bm*, and with apex convex, nearly perpendicular to the two veins CuA and CuP, unlike *Pouillonhybos* (Smith, 1969: figs 127-128, 130; Yang & Grootaert, 2004; Solórzano-Kraemer et al., 2020).

The fossil shares many traits with the subfamily Ocydromiinae, in which cell *cua* is shorter than or about as long as cell *bm*, with its outer angle obtuse; the postpedicel shorter than the arista-like stylus; a cell *dm* present; and the proboscis oriented ventrad, all as in *Pouillonhybos* (Sinclair & Cumming, 2000, 2006; Wahlberg & Johanson, 2018). In addition, ocydromiines also have an epandrium with an apical pair of articulated surstyli, another trait apparently present in *Pouillonhybos*, pointing to a placement within the subfamily for this new Cretaceous genus.

Within this subfamily, *Leptopezella* Sinclair & Cumming, 2007 has no discal cell, a pterostigma, cell *cua* clearly shorter than *bm*, and no metatibial extension, and is therefore quite different from *Pouillonhybos* (Sinclair & Cumming, 2007). *Abocciputa* Plant, 1989 and *Chvalaea* Papp & Földvári, 2001 differ from *Pouillonhybos* in that cell *cua* is significantly shorter than cell *bm*, there is no trace of M_2, and R_{4+5} is not parallel to M1 (Plant, 1989; Papp & Földvári, 2002; Shamshev et al., 2017), and the genera *Austropeza* Plant, 1989, *Pseudoscelolabes* Collin, 1933, and *Leptodromiella* Tuomikoski, 1936 also have cell *bm* much longer than cell *cua* (Tuomikoski, 1936; Collin, 1926, 1928, 1933; Chvála, 1983; Plant, 1989). *Oropezella* also has a rather long cell *dm* and quite short veins emerging from it, unlike

Pouillonhybos (Chvála, 1983; Ale Rocha, 2007). In the genus *Stylocydromia* Saigusa, 1986 there is a long cell *dm*, while the base of Rs is much closer to h than to r-m, unlike the condition in *Pouillonhybos* (Saigusa, 1986). The genus *Leptopeza* Macquart, 1827 has a rudimentary M_1 and cell *bm* much longer than cell *cua* (Chvála, 1983), while in *Ocydromia* Meigen, 1820, the stylus is supra-apical rather than apical in *Pouillonhybos*, and moreover cell *bm* is much longer than cell *cua* and there is no trace of a third vein emerging from *dm* (Chvála, 1983). *Apterodromia* Oldroyd, 1949 shares with *Pouillonhybos* a cell *cua* nearly as long as *bm*, but it has an anal area much more reduced than *Pouillonhybos* and a well-defined M_2 (Sinclair & Cumming, 2000). *Neotrichina* Sinclair & Cumming, 2000 has the stylus scarcely as long as the postpedicel, three veins emitted from *dm* that reach the wing margin, cell *cua* much shorter than *bm*, an anal vein almost complete to the wing margin, CuA closing *cua* almost straight, all quite distinct from the character states present in *Pouillonhybos*; also some species of *Neotrichina* have the metatibia dilated apically but without a lateral expansion, and therefore unlike that in *Pouillonhybos* (Collin, 1933; Sinclair & Cumming, 2000). *Hoplopeza* Bezzi, 1909 and *Scelolabes* Philippi, 1865 can be excluded from having any affinity with the new fossil genus because they have Rs short, arising near the apex of cell *bm*, and cell *cua* much shorter than *bm* (Collin, 1933; Rafael, 1995; Sinclair & Cumming, 2000). Lastly, *Leptodromia* Sinclair & Cumming, 2000 has cell *cua* two-thirds length of cell *bm* and a short M_1 that does not reach the wing margin (Bezzi, 1904; Sinclair & Cumming, 2000).

Among known extinct genera, the Eocene Baltic amber genus *Palaeoleptopeza* Meunier, 1908, was considered as near to "*Leptopeza* but with spinose hind femora" by Melander (1928: 371), and differs from *Pouillonhybos* in that the postpedicel is as long as the stylus, R_{2+3} is distinctly arcuate, and M2 is more clearly defined as a fuscous nebulous trace (Meunier, 1908: pl. 7, fig. 15, pl. 8, fig. 4). *Ecommocydromia difficilis* Schlüter, 1978 is the

unique Cretaceous taxon currently attributed to the Ocydromiinae; it is based on an incomplete specimen in amber with numerous characters of wing venation missing (in particular, the relative positions of r-m, base of Rs, and h are unknown), rendering it impossible to determine if this assignment is valid or whether it might belong to the Dolichopodidae. It has three long veins emerging from an elongate cell *dm*, which is quite unlike any other Ocydromiinae. The cells *bm* and *cua* are not preserved, and we believe that attribution to Ocydromiinae is difficult to justify (Schlüter, 1978: figs 86-89). *Ecommocydromia difficilis* is perhaps best considered as incertae sedis until more completely preserved specimens are recovered. The Eocene Baltic amber genus *Meghyperella* Meunier, 1908 was considered by Melander (1928: 370) as "apparently related to *Leptopeza*" (Ocydromiinae), and possibly a "predecessor of *Stenoproctus*" (Hybotinae). It differs from *Pouillonhybos* in the exceptionally short stylus (Meunier, 1908), and needs to be revised. Evenhuis (1994) listed it among the fossil 'Empididae'. Note that the alleged Oligocene hybotine genus *Eternia* Martins-Neto et al., 1992 is based on a poorly preserved fossil, but it preserves *cua* as long as *bm* with an obtuse outer angle, suggesting it belongs to the Ocydromiinae (Martins-Neto et al., 1992). Lastly, the putative Oligocene hybotine genus *Tremembella* Martins-Neto et al., 1992 is based on an exceptionally poorly preserved specimen and until more complete material is discovered it remains impossible to compare with the other genera.

The only other Hybotidae from Burmese amber is *Electrocyrtoma burmanica* Cockerell, 1917, a genus that differs from *Pouillonhybos* in the absence of cell *dm*, a much broader cell *bm*, and a cell *cua* much shorter than *bm* (Cockerell, 1917: fig. 5). Melander (1928: 368) indicated that *Electrocyrtoma* resembled *Bicellaria*, while Grimaldi & Cumming (1999: 51) considered it as belonging to Tachydromiinae.

5. Conclusions

Pouillonhybos is the first ocydromiine from Burmese amber and probably the only definitive representative of this subfamily from the Cretaceous. Modern Ocydromiinae are predators (Chvála, 1976), and like other hybotids often hold their prey with the hind legs while feeding. However, no living ocydromiines have a massive prominence on the metatibia like the one present in *Pouillonhybos*. This structure, together with the stout setae and spines on the metafemur, erect and spine-like setae on ventral surface of mesofemur, and setae on the other femora and tibiae, coxae, and abdomen, strongly suggest that *Pouillonhybos* was a predator who, like surviving relatives, captured and hold prey with its hind legs. The hybotine genera *Hybos*, *Syndyas*, and *Syneches* have raptorial hind legs (Grootaert, 1996), with strong spines on the metafemur but no prominent extension on the metatibia. Some species of *Lactistomyia* also have raptorial hind legs with a metatibial lateral extension, albeit situated in a distinctly more proximal position than that of *Pouillonhybos* (Ale-Rocha, 2008). *Afrohybos* has also a highly modified hind leg with a ventral extension of the metafemur and strong spines on the metatibia (Smith, 1969: fig. 96), while the hybotine genus *Syneproctus* has a metatibia with an apical extension most analogous to that of the fossil, but quite a bit smaller than that of *Pouillonhybos*.

Many Hybotidae and Dolichopodidae have raptorial fore and/or mid legs with greatly modified femora and/or tibiae, and some dolichopodids have a strong spine on an apical extension of the meso- and/or metatibia and/or structures on the metabasitarsus, resembling the metatibial extension of *Pouillonhybos* and *Syneproctus* (Bickel, 1985: figs 7-8; Zhu et al., 2005; Runyon, 2008; Grichanov & Brooks, 2017). It is clear that not only various leg modifications have evolved convergently among empidoid lineages for subduing and handling prey, but such traits also appeared in the early phases of their diversification as evidence by their presence in at least one Cretaceous ocydromiine. The special shape of the

legs of *Pouillonhybos* suggests that it was catching its preys during flight, as for the extant Ocydromiinae (Daugeron, 1997).

Many Empidoidea are well-known for their complex mating behavior, with gifts to the female and semaphore behaviors. Nevertheless, after Downes (1969: 290), both sexes of 'the extant Hybotinae and some Ocydromiinae' .... 'capture prey and the feeding habits have no relationship to the flight in the mating swarm'. Even if the extant Ocydromiinae are making swarms without mating (Daugeron, 1997), in absence of information on the morphology of the female of *Pouillonhybos*, it is not possible to infer hypotheses about the mating behavior in this ancient Hybotidae.

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512 **FIG. 1.** ***Pouillonhybos venator*** Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
513 MHNE.2020.7.1. A, habitus, ventral view. B, wing, arrow base of vein M2. Scale bars = 1
514 mm.

515 **FIG. 2.** ***Pouillonhybos venator*** Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
516 MHNE.2020.7.1. Hind leg, c.s. coxal seta, bt. basitarsus, f. femur, t. tibia, s. spur. Scale bar =
517 1 mm.

518 **FIG. 3.** ***Pouillonhybos venator*** Ngô-Muller, Engel, & Nel, gen. et sp. nov., holotype
519 MHNE.2020.7.1. A, head, above. B, male terminalia, lateral view; ce cercus, ep epandrium,
520 ph phallus. Scale bar = 0.5 mm (A), 0.1 mm (B).
521